# 22. On the Nature of the Lateral Muscle in Teleostei.

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(Text-figures 1–3.)

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## 1. Introductory.

During the past two years my research hours have been largely devoted to a study of the myology of the pectoral girdle and fin of fishes, and recently the Teleosteans have more particularly occupied my attention. As the musculature of the limbs is entirely derived from the so-called lateral muscle, it is desirable, in the first instance, accurately to comprehend the nature of the lateral muscle.

That the primitive composition of the lateral muscle, seen only in the embryonic condition of living fishes, becomes highly modified in the adult Teleostean is beyond doubt; but it is difficult to reconcile the views of various authors, some of whom interpret it in terms of two superimposed layers and others in terms of one layer. It would be obviously unwise to advance to a description of the myology of the limbs while this fundamental question is left undecided. To uphold the single-layer theory of thê lateral muscle in Teleostei is, then, the primary object of the present paper.

The complex series of cranial muscles is also derived from the lateral muscle, but the secondary modifications which they have undergone render highly problematical any conclusions based on their arrangement. For this reason the cranial muscles will only receive passing consideration. The brunt of the discussion will be focussed upon that portion of the lateral muscle which lies behind the pectoral girdle; and, in particular, upon the caudal region, which is generally accepted as the least modified.

Though not a primary part of my research, the conclusions advanced below are the outcome of it; and they are offered as a preface to a section of an original morphological study.

I wish to record my gratitude to the Carnegie Trust, whose

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grant in aid of research provided me with an image-erecting binocular microscope, invaluable in tracing the intricate courses of muscle-fibres, giving comprehensive stereoscopic views of the muscle such as are unobtainable by simpler forms of optical apparatus.

## Historical.

Owen (8) emphasizes the fact that the lateral muscle is essentially an aggregate structure formed of a series of transverse muscles (myomeres). The divisions of the lateral muscle which he cites are based on the directions of the myocommata ("tendinous insertions"); but he does not regard these as having any true morphological value. The carinales, however, are regarded as entities. I can find nothing in Owen's writing to show that he regarded the lateral muscle as divisible into two layers.

Humphry (4) recognises a true division of the lateral muscle, by a septum passing inwards beneath the lateral line, into a dorsal and a ventral moiety. His subsequent divisions of these moieties are based on the directions of the myocommata; at the same time he states that when these divisions are traced forwards to their insertions they become completely severed one from the other. The red fibres occur superficially on either side of the lateral line. The latero-ventral portion of the muscle (see table) is divided by the direction of its component fibres into a superficial layer (obliquus externus) and a deep layer (ob. internus), but there is no septum between these two layers. In this portion a third layer was noted in certain Teleosts (Bream, Dace), which, from its position beneath the ribs, was regarded as a possible homologue of the transversalis layer of Amphibia. Similar changes in the direction of the fibres enabled Humphry to distinguish three areas of the mesio-ventral portion, two superficial and one deep, but these again were not defined by fasciæ.

Gegenbaur (3) also recognises a horizontal plane of division at the lateral line whereby a dorsal is separated from a ventral moiety. He proceeds to divide these moieties in terms of cones, complete and incomplete, which are revealed in sections of fishes. It is desirable here to draw attention to a discrepancy which is displayed in the illustration fig. 276, A, which represents the time-honoured caudal section of a Mackerel, originally drawn by J. Müller, of which Owen (amongst others) has made use. Gegenbaur's description of this section is perfectly lucid, and more precise than Owen's; but, unfortunately, he has added a diagram of the superficial arrangement of the myocommata (fig. 276, B), wherein, if we may judge by the lettering, he represents the upper cones (*a*) as identical with the cones seen in section in fig. 276, A*a*. In reality the superficial cones are directed posteriorly and their apices represent the angles which the uppermost superficial fibres of the true cones make with fibres of the incomplete cones (which are directed downwards and backwards), whereas the true cones are directed anteriorly and, being deeply seated, are not visible superficially. Moreover, the apices of the superficial cones are of necessity situated in a higher horizontal plane than those of the true cones.

The five longitudinal portions of the lateral muscle which McMurrich (7) derived from his investigation of *Amiurus* are equivalent to various areas described by previous authors. This is indicated by the positions which they take in the above table. The author implies that the classification is only of empirical value. His divisions are based upon the superficial appearance of the muscles, and upon the extent of their origins. He does not recognise a clear division beneath the lateral line, nor is there any suggestion of stratification in any portion of the lateral mvscle.

Maurer (6) divides the lateral muscle into two portions, a dorsal and a ventral, separated by the lateral line. The dorsal portion is outside the sphere of his investigation, the ventral he proceeds to split into layers.

If the red fibres * immediately ventral to the lateral line be removed, a stout muscular layer is observed whose fibres run obliquely, from forwards and upwards to backwards and downwards (*i. e.* in the same direction as those of the obliquus externus of Amphibia). The outermost layer of this muscle runs from septum to septum, the inner from rib to rib; since, however, the direction of the fibres does not change, the two layers are regarded as comprising a single muscle, the obliquus externus †.

Ventrally the origins of the fibres of this muscle change so as to resemble those of the obliquus internus of Urodeles ‡, while the fibres which meet in the mid-ventral line their fellows of the opposite side go to form a rectus.

Returning to the area of the ventral muscle immediately below the lateral line, where the fibres take the direction of the obliquus externus of Amphibia, if the superficial fibres be removed a deep layer is found whose fibres slant in the opposite direction (*i. e.* from forwards and downwards to backwards and upwards, like those of the obliquus internus of Amphibia). These fibres form a thin deep stratum running from rib to rib §. There is no mention, however, of a fascia separating the deep from the superficial stratum.

Beneath the above layers is yet a third, in *Chondrostoma*, at least; this is spoken of as a thick one covering the peritoneum ||.

The rectus is not, he says, developed as a costal muscle, rather as a ventral part of the primary belly-musculature ¶.

* The occurrence of these red fibres is more fully described on p. 326.

† The equivalent of Humphry's latero-ventral (surface) portion.

‡ This and the superficial layer of the next form the "pectoralis" of Humphry.

§ Equivalent in all respects to Humphry's "obliquus internus."

|| This is apparently equivalent to the transversus stratum which Humphry observed in the Bream and Dace. Nevertheless, Maurer states that the transversus properly so called is absent in all fishes.

¶ From which I gather that this muscle is regarded as being continuous dorsally both with the obliquus externus and with the obliquus internus. It thus included the "rectus" and ventral portion of "pectoralis" of Humphry.

Here we have an exposition of the two-layer theory of the lateral muscle of Teleostei, differing in few points from that advanced by Humphry.

Wiedersheim (9) describes the completeness of the division of the dorsal and lateral moieties of the lateral muscle by a connective tissue septum extending from the axial skeleton to the integument at the region of the lateral line. Only one layer of muscle is recognised.

With Knauer (5) we are brought into contact with a new view of the lateral muscle. It is divided longitudinally into two main portions which are defined according as they arise from (*a*) the head (Rückenmuskulatur) or (*b*) the neck (Bauchmuskulatur). The division at the lateral line, though complete, is only regarded as being of secondary importance. The oblique line in the table severing the back musculature from the belly musculature indicates the author's contention that the former gradually pushes its way over the latter as we proceed in an antero-posterior direction. Finally, in the posterior abdominal region the back musculature comes completely to enclose the diminishing belly musculature; and in this area a true stratification of the body-wall is realized. His lateral line muscle is synonymous beyond doubt with the "red fibres" of other authors.

Text-figure 1.

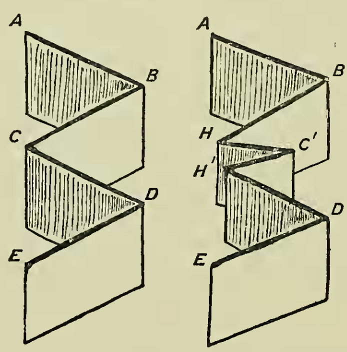



Diagram to illustrate the apparent (ABCDE) and the real (ABHC'H'DE) construction of a myomere. (After R. Chevrel.)

Dietz (2) bases his division of a Teleostean myomere, and hence of the lateral muscle, on the transverse septum extending beneath the lateral line. His subsequent divisions are due to the direction of the myocommata. He proceeds to investigate myomeres from various parts of the body, and shows how the pleuro-dorsal portion gradually becomes emancipated from the pleuro-ventral as we proceed antero-posteriorly; with this is correlated the change of a single half myomere, dorsal or ventral, from a single bend to a double bend *.

Chevrel (1) has given a lucid description of the conical, or pyramidical, structure of the myomeres forming the lateral muscle. His diagram illustrative of the apparent and the real structure of a single typical Teleostean myomere is reproduced here (text-fig. 1). At B is seen the dorsal posterior pyramid, at H the anterior dorsal pyramid, at H' and D the ventral pyramids, while C indicates the lateral line. It is only necessary to add that in the abdominal region the dorsal moiety (portion épiaxiale) alone exhibits this double evagination; the ventral (portion hypoaxiale) is ribbon-like. Chevrel recognises a horizontal septum dividing completely a dorsal from a ventral moiety; but there is no mention of stratification in any area of the lateral muscle. The carinales (m. grêles) are the homologues behind the pelvis of the rectus which is found in the thoracic region.

## The Author's Observations.

Having now stated the principal views extant as to the divisions of the lateral muscle in Teleostei, the conflicting nature of these becomes patent. I shall next proceed to formulate a classification of the parts of the lateral muscle, retaining such features as are agreed upon by the majority of the investigators whose work I have studied, and discarding those which I find to be incapable of general application. In this classification no new terms will be introduced, preference being accorded to those which are deemed most descriptive. I wish it clearly to be understood that I regard any such classification, in the light of our present limited knowledge, as essentially empirical and tentative.

That the so-called lateral muscle of fishes is, more strictly speaking, a sequence of serially homologous transverse muscles (myomeres) is the fundamental starting point upon which all investigators are agreed. Setting this fact in the background, but never letting it completely out of sight, let us proceed first to map out the superficial divisions of this muscle in a Teleostean, and then to prove by dissection the morphological value of these divisions.

No specified type has been taken; but the description, and herein lies what merit it possesses, is so generalised as to apply to the majority of Teleostean fishes. Exceptional cases will be cited wherever practicable.

### (1) *External Conformation.*

The most obvious longitudinal division giving rise to a dorsal and a ventral moiety is formed by the passage of the lateral line. Upon this point there is but one voice.

* This process can be very clearly followed in Knauer's drawings of Salmon sections, *op. cit.* pl. iii. figs. 15–19.

Tabulated Summary of the

| | Owen (8). | Humphry (4). | | Gegenbaur (3). | McMurrich (7). | Maurer (6). | |
|---|---|---|---|---|---|---|---|
| | | *Superficial.* | *Deep.* | | | *Superficial.* | *Deep.* |
| | *Supra-carinalis.* | | | | *1st Portion.* | | |
| Dorsal Moiety. | Dorsal Section. | Mesio-dorsal Portion. | | Incomplete Cones (directed backwards). | 2nd Portion. | Dorsal Portion. | |
| | Dorsal Middle Section. | Latero-dorsal Portion. | | Entire Cones (directed forwards). | | | |
| Lateral line. | | *Red fibres.* | | | | *Red fibres.* | |
| | | *Red fibres.* | | | | *Red fibres.* | |
| Ventral Moiety. | Ventral Middle Section. | Latero-ventral Portion. Obliquus externus. | Obliquus internus. | Entire Cones (directed forwards). | 3rd Portion. | Obliquus externus. | Obliquus internus. |
| | Ventral Section. | Mesio-ventral Portion { Lat. dorsi; Pectoralis. | Rectus. | Incomplete Cones (directed backwards). | 4th Portion. | Diagonal fibres (sloped as in Obl. internus). | |
| | | | | | | Rectus. | |
| | *Infra-carinalis.* | *Carinales.* | | | *5th Portion.* | | |

With regard to the dorsal moiety, of the writers quoted above, McMurrich, Maurer, Wiedersheim, and Knauer see no reason for a further subdivision. The remainder, however, favour a division, but are divided as to the nature of that division, Owen and Humphry using the external appearance as a basis, while Gegenbaur, Dietz, and Chevrel refer to it in terms of internal cones (the difference will subsequently be shown to be of less degree than at first sight appears). The myocommata of the dorsal moiety in the trunk region are V-shaped, the apex of the V being directed posteriorly. The inclination of the V varies from an acute to an obtuse angle. Between two successive myocommata the muscle-fibres have often been said to run parallel to the long axis of the body. This is the case in the middle region, but, in the arms of the V, the fibres gradually become more or less inclined in the same direction as the arms; that is to say, if produced, the fibres in the upper and lower arms would meet behind the V. With Humphry, we will denote that portion of the dorsal moiety which contains the upper backwardly directed arms of the V as the mesio-dorsal portion, and that which

Views of the Authors cited.

| Wiedersheim (9). | | Knauer (5). Superficial. | Knauer (5). Deep. | Dietz (2). | Chevrel (1). | |
|---|---|---|---|---|---|---|
| Dorsal Portion. | | Straight Back-muscle. | | Dorsal proper. | Dorsal Portion. | Posterior, external, or superficial Pyramids. |
| | | Back (Rücken) Musculature. | | Pleuro-Dorsal. | | Anterior, internal, or deep Pyramids. |
| | | *Lat. line muscle.* | | | | *Red fibres.* |
| Ventral Portion. | | *Lat. line muscle.* | | | | *Red fibres.* |
| | Analogue of Obliquus. | Oblique Back-muscle. | | Pleuro-Ventral. | Ventral Portion. | Anterior, internal, or deep Pyramids. |
| | Analogue of Rectus. | Belly (Bauch) Musculature. | Oblique Belly-muscles. | Ventral Proper. | | Posterior, external, or superficial Pyramids. |
| | | (Rectus). Straight | Belly-muscles. | | | |
| | | Muscles grêles. | | | | |

contains the lower backwardly directed arms as the latero-dorsal portion (see text-fig. 2, *M.D.*, *L.D.* p. 331). In the trunk region there is no distinction between the mesio-dorsal and the latero-dorsal portions except in the direction of their fibres, and, even then, the differently directed fibres are connected by a transitional area. Tracing these portions forwards to the back of the head the two are found gradually to be severed from one another; strong fasciæ separate them; their transverse divisions begin successively to fade and disappear; and, finally, they are inserted on the skull, the mesio-dorsal portion on its roof (supraoccipital), the latero-dorsal portion on its side (exoccipital and otic recess) and on the post-temporal; the last named gives off a superficial branch to the supraclavicle (*Blennius pholis*) or to the cleithrum itself (*Cottus scorpius*, where it is attached to the posterior border of the backwardly directed spine in which that bone ends).

In the little gobiiform fish, *Periophthalmus*, the mesio-dorsal portion is attached to the upper border of the post-temporal as well as to the supraoccipital; but this so far as my observations go is an exceptional occurrence.

In the majority of Teleosteans a small muscle is cut off from the latero-dorsal portion immediately above the lateral line. From the distinctive coloration which it frequently presents it has become known as the "red muscle" or "red fibres." It is not merely differentiated from the latero-dorsal portion by the colour of its fibres, or even by their direction, which is parallel to the long axis of the body (whereas those of the main muscle are directed slightly upwards and backwards); but a distinct fascia separates it in each myomere (see text-fig. 3, *r.f.* p. 334). A similar "red muscle" is cut off from the latero-ventral portion immediately below the lateral line. The "red muscle" is mentioned by Chevrel; we have seen that it was also recognised by Maurer. Chevrel states in another part of his text that this muscle is constant neither in presence, nor in form, nor in tint, nor even in its relations with the lateral nerve. Further, in Humphry's paper (*op. cit.* p. 294) the following words in reference to fishes appear in a footnote:—" . . . . . and the lateral furrows are commonly occupied by muscular fibres which bear the transverse septa, but which are more closely connected with the skin, and peel off with it more easily than the rest of the lateral muscle. These fibres are more vascular than ordinary muscular fibres; and in a piece which I examined from a Dace they contained more oil than the other muscles. Stannius (Handbuch der Zootomie (2), 112) says that they, in addition, present microscopically the appearance of tissue in process of conversion into muscle. I did not find that to be the case. With the exception of the excess of oil, they represented the usual microscopical characters of striped muscle." Such observations as I have made go to support Humphry's statements. The "red muscle" gradually disappears anteriorly, so that it never reaches the shoulder-girdle.

Turning next to the ventral moiety, we find, in the trunk region, an exact repetition of the condition that has been described for the dorsal moiety. Following Humphry's nomenclature, which we have used above, let us designate the area immediately below the lateral line, comprising the backwardly and downwardly directed arms of the V-shaped myocommata, as the latero-ventral portion, and the area between this and the mid-ventral line (or the infracarinales muscles, where such are present) as the mesio-ventral portion (see text-fig. 2, *L.V.* and *M.V.*). It will be apparent, on turning back to the tabulated summary of the views of the various authors, that this division of the ventral moiety of the lateral muscle meets with more general recognition than does a corresponding division of the dorsal moiety. Tracing these portions forward to the shoulder-girdle, we find that the apices of the backwardly and downwardly directed V-shaped myocommata rapidly approach the lateral line: in other words, the latero-ventral portion rapidly disappears. McMurrich states that this portion (his "3rd portion") disappears in *Amiurus* before reaching the shoulder-girdle; such is the case in some other Teleosteans, but in the majority which I have examined a small bundle of fibres, undoubtedly the continuations of the latero-ventral portion, are attached to the upper extremity of the cleithrum. At its point of attachment and for a short distance behind, the latero-ventral portion is actually severed from the mesio-ventral; though, further back, the two are continuous, just as are the mesio-dorsal and latero-dorsal portions. With the decrease in width of the latero-ventral portion, the mesio-ventral portion increases so that it becomes attached to the whole length of the cleithrum, except at the dorsal extremity of that bone, and to the coracoid in part. There exists, however, a triangular area, composed of connective-tissue traversed by a few muscle fibres, beneath the pectoral fin; this triangle has its base on the cleithrum, consequently there appear to be two main insertions of the mesio-ventral portion on the cleithrum.

On the ventral surface in the anterior region the fibres of the mesio-ventral surface meet their fellows of the opposite side; the fibres are here arranged parallel to the long axis of the body, which has led some authors to regard them as homologous (Humphry and Maurer), or, at least, analogous (Wiedersheim) to the rectus abdominis of the higher vertebrates. In Teleosteans whose pelvic fins are thoracic or jugular in position the ramifications of this portion of the lateral muscle show remarkable variety. To describe these ramifications in detail would only serve to confuse the issue of the investigation in hand; but it is worthy of note that, in every example which I have had occasion to examine, a bundle of fibres from the mesio-ventral portion of the lateral muscle runs forward without interruption to be inserted on the hypohyal.

Knauer (**5**) figures the lateral muscle of the Gurnard in the area just behind the shoulder-girdle (Pl. iii. fig. 20). In this illustration the mesio-ventral portion (Bauchmuskel) is depicted as gradually disappearing towards its posterior extremity, and in the text he says that in the anal region this muscle, with its straight-running fibres, is reduced to a small strip on either side; further, that these strips fuse with the latero-ventral portions (Rückenmuskulatur) behind the anus. This is not indicated in the figure, where the mesio-ventral portion appears to die out in the anal region; *Trigla*, however, with its flattened ventral surface is not, perhaps (with deference to the author), the best type of Teleostean fish for representing in side view the entire extent of this portion of the lateral muscle. A little distance behind the anus the mesio-ventral portion entirely disappears, and the latero-ventral portions (schrägen Rückenmuskel) of either side are separated by the anal fin. I had also used Gurnards* in my investigation of the lateral muscle. Since reading Knauer's paper, I have examined them again most

* *Trigla gurnardus*, whereas Knauer's specimen was *T. hirundo*.

carefully, and with the result that I still maintain that the mesio-ventral portion is continued to the extremity of the tail in that species just as has been described above for Teleosteans in general.

There remain yet to be considered the small cylindrical muscles known as carinales. These may be absent, and, when present, exhibit considerable variety in their extent. The upper pair, supracarinales, run parallel to one another along the mid-dorsal line, separating the mesio-dorsal portions of either side of the main lateral muscle-masses. They take origin on the occiput in the Cod (Owen), whence they run to the first dorsal, and reappear again in the interspaces between the dorsal fins; in *Periophthalmus* they arise slightly behind the skull from the neural spines, and traverse the interspaces between the dorsal fins; in *Amiurus* they only appear behind the first dorsal fin, and McMurrich describes them as "formed by the union of slips arising by tendons from the spinous processes." They are separated by strong fasciæ from the main masses of the lateral muscles, but retain their original metameric segmentation. Functionally they act, according to their position, as elevators or depressors of the dorsal fin-rays. They may be regarded as specialised modifications of the lateral muscle, just as are the other fin-muscles.

The lower pair, infracarinales, are similar in nature to the foregoing muscles, and, when present, divide the mesio-ventral portions of either side of the lateral muscle. Both Owen and McMurrich, who have described them, agree that they may be divided into an anterior and a posterior section. The latter extends from the posterior end of the anal fin to the base of the caudal, and between the two anal fins where such occur. The former extends from the anterior end of the anal fin to be inserted on the posterior face of the pelvic bone (ischium, Owen); hence they describe it as the "retractor ischii," and Owen goes so far as to describe in the Perch the "protractor ischii" as a still further anterior prolongation of the same muscle.

A difficulty now arises. In many Teleosteans, especially in forms whose pelvic girdles are situated far forward, the "retractor ischii" a short distance behind its origin on the posterior aspect of the pelvic bone becomes inseparably fused with the mesio-ventral portion of the lateral muscle; or, in other words, part of the mesio-ventral portion forms in many cases the "retractor ischii." It would seem that the latter condition is more primitive than that where the "retractor ischii" is composed of a carinalis muscle, which has been noted as a secondary modification of the lateral muscle. Yet the "retractor ischii" composed of an infracarinalis occurs for the most part in Teleosteans with abdominal pelvic fins, that is to say, in the more primitive forms; and *vice versa*, the (presumably) more primitive condition of the "retractor ischii" occurs in the more specialised Teleosteans. This interesting anomaly is beyond the scope of the present investigation; it recalls frequent analogous occurrences in the evolution of animals, and is merely noted here as a bye-way which might repay exploration.

Summary of the external divisions of the lateral muscle:—

1. Supracarinalis.
2. Dorsal moiety.
   (*a*) Mesio-dorsal portion.
   (*b*) Latero-dorsal portion.
3. "Red Muscle."

(Lateral Line.)

4. "Red Muscle."
5. Ventral moiety.
   (*a*) Latero-ventral portion.
   (*b*) Mesio-ventral portion.
6. Infracarinalis.

(2) *Internal Structure.*

In the foregoing section we have named the outstanding superficial divisions of the lateral muscle in Teleosteans. Let us now proceed to prove by dissection to what extent these external markings are evidence of internal structure. Enough has already been said of the carinales and of the "red muscles" to show that these are specialised offshoots from the lateral muscle; and, since all the authors who have mentioned them are agreed as to their morphological value, it would be superfluous to treat of them at greater length in the present paper; suffice it to say that there is no question of their division into more than one stratum, nor are they themselves regarded in the light of strata, deep or superficial, of the lateral muscle. Let us concentrate our attention upon the dorsal and ventral moieties of the main mass of the lateral muscle.

With the exception of Owen and McMurrich, all the authors whom I have quoted maintain the completeness of the division at the lateral line. Dissection shows a well-marked septum running continuously from beneath the lateral nerve to the bodies of the vertebræ. The lateral line, then, must be regarded as the external evidence of a true horizontal division of the lateral muscle.

Having established this fundamental division, let us enquire to what extent the dorsal moiety may legitimately be subdivided. It has been shown that it comprises superficially, (*a*) a mesio-dorsal portion, in which the fibres of each myomere are directed from above anteriorly to below posteriorly, and (*b*) a latero-dorsal portion in which the fibres take the opposite direction. On stripping the superficial fibres from the latero-dorsal portion of a typical myomere such as occurs in the caudal region, it is found that the direction of the underlying fibres gradually changes so as to become, first, parallel with the long axis of the body, and then, very near to the vertebral column, from above anteriorly to below posteriorly (like those of the superficial area of the mesio-dorsal portion).

It is this change in direction of the fibres which led Humphry and Maurer to distinguish two layers in the ventral moiety of the lateral muscle. If Chevrel's account of the internal structure of a myomere has been followed, the reason for this change in direction of the fibres will be perfectly clear. Since the ventral half of the dorsal moiety of the myomere takes the form of a pyramid with its apex directed anteriorly, of the fibres running from the apex the uppermost ones may be expected to take a direction from below anteriorly to above posteriorly, and the lower ones from above anteriorly to below posteriorly; and this is indeed the case. Moreover, since the apex is directed inwards and downwards, only the outer upper faces of the pyramids on which the fibres are directed from below anteriorly to above posteriorly, is visible externally, and has been designated the "latero-dorsal portion" in our superficial examination. The lower face, on the other hand, in which the fibres are directed from above anteriorly to below posteriorly, is hidden beneath the surface.

Similarly, the portion which has been designated "mesio-dorsal" in our superficial examination represents the outer face of a backwardly directed pyramid.

It has already been mentioned that, just behind the head, near the insertions of the mesio-dorsal and latero-dorsal portions of the lateral muscle, these two masses are divided. The division is not merely superficial, but extends usually throughout their depth; though in some forms (*Cottus scorpius*) a certain number of strands from their deeper contiguous faces serve to connect them almost up to the point of their insertions.

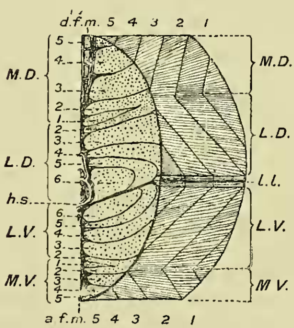
The above description of the arrangement of the dorsal moiety of a myomere of the caudal region applies equally well to the ventral moiety in the same region, only the direction of the apices of the pyramids is reversed, the dorsal one being directed anteriorly, the ventral posteriorly. Here, again, only the outer face, but in this case the lower, of the anteriorly directed pyramid, with its fibres running from above anteriorly to below posteriorly, is visible externally, where it is recognised as the "latero-ventral portion" of our superficial examination; while beneath it lies the upper face, in which the fibres run in the opposite direction, namely, from below anteriorly to above posteriorly. Hence the explanation of the description in this portion of the lateral muscle of two superimposed strata, equivalent respectively to the obliquus externus and obliquus internus of higher vertebrates, advanced by Humphry and Maurer.

In the abdominal region, where the walls of the ventral moiety are of necessity thin, the conical structure of the myomere is lost. The latero-ventral portion throughout its depth contains fibres which are directed from above anteriorly to below posteriorly, at least in its most anterior area. It acquires its characteristic conical structure, however, considerably further forward than does the mesio-ventral portion. The latter contains fibres which are directed from below anteriorly to above posteriorly on the lower parts of the flanks; but, as noticed above, the fibres of the ventral surface change in direction the nearer they approach to the mid-ventral line so as to be disposed parallel to the long axis of the body. I have failed in every instance to find a septum, such as is described by Knauer, dividing the mesio-ventral portion into two superimposed layers.

It has been stated above that a strand of the mesio-ventral portion is prolonged anteriorly to be inserted on the hypo-hyal. This strand, together with the hyo-cleithrale *, constitutes the neck musculature. Knauer (5) recognised these parts of the neck musculature, and adds the following note (*op. cit.* p. 11):—

"Die Angabe Schneiders, dass sich der *Sternohyoideus* * aus zwei der Länge nach zusammengewachsenen Muskeln (Hyodorsalis und Hyoventralis) zusammensetzt, die als Fortsetzung des Rückenmuskels und des Rectus zu betrachten sind, ist dadurch zu verstehen, dass Schneider offenbar schon die oben erwähnte Fortsetzung der inneren Schichte (von ihm als Rückenmuskulatur aufgefasst) in die Halsmuskulatur bemerkte."

Text-figure 2.




Transverse section through the caudal region of a typical Teleostean with the contiguous body-surface, to show the relations to one another of six consecutive myomeres. The right side of the figure represents the anterior portion of the section. (Generalised, mainly from *Cottus scorpius.*)

*M.D.*, Mesio-dorsal portion; *M.V.*, Mesio-ventral portion; *L.D.*, Latero-dorsal portion; *L.V.*, Latero-ventral portion; 1–6, consecutive myomeres, the first is anterior; *h.s.*, horizontal septum; *l.l.*, lateral line (with "red fibres" on either side of it); *a.f.m.*, anal fin-muscle; *d.f.m.*, dorsal fin-muscle.

I, too, have noted this double condition of the hyo-cleithrale in certain Teleosteans (*Lophius*, *Trigla*, *Zeus*). My observations

* A revised term more accurately descriptive of the muscle hitherto known as hyo-clavicularis (synon. *Stenohyoideus*, *Cervicalis profundus*, etc.).

tend to indicate that the division line is horizontal rather than tangential; that is to say, they support Schneider's view.

Chevrel's diagram of the pyramidical disposition of a caudal myomere has been reproduced on p. 322 (text-fig. 1); the accompanying illustration (text-fig. 2) will serve to convey a more realistic view of the manner in which the pyramids fit one into the other. Let us follow in turn the course of six myomeres represented in the text-figure.

*First myomere.*—This is seen at the surface on the right of the text-figure (1). In the mesio-dorsal portion (*M.D.*) its fibres are directed from above anteriorly to below posteriorly, in the latero-dorsal portion (*L.D.*) the fibres are directed from below anteriorly to above posteriorly; in the ventral moiety (*L.V.* and *M.V.*) this sequence is repeated. The dorsal moiety is separated from the ventral by the lateral line (*l.l.*) and by the "red fibres" on either side of it. Looking into the section, we find the first myomere (1) in the form of an acute angled triangle with its base abutting on the vertical septum, in which run dorsally the neural spines and ventrally the hæmal spines; it presents a similar appearance both in the dorsal and ventral moieties.

*Second myomere.*—Seen at the surface immediately behind the foregoing, it takes a similar course; the posteriorly directed apices of its V-shaped bends are broken, however, by the section. Following its course into the section we find that it presents a V-shaped mass which bestrides the triangular section of the first myomere.

*Third, fourth, and fifth myomeres.*—These are seen externally, each at four points, as a series of gradually vanishing segments of the V-shaped arms (the fifth myomere, however, does not appear superficially in the central region). In section each presents four quadrangular faces, two above and two below the horizontal septum. Near the middle line the faces become curved, so that they present a convex surface to the exterior and a concave surface to the interior.

*Sixth myomere.*—This does not appear superficially, but is seen as a roughly triangular mass on either side of the horizontal septum. The base of the dorsal triangular mass rests against the body of the vertebra, that of the ventral one against the hæmal arch. The outer angles of these triangles, unlike those of the sections of the first myomere, are rounded off, and fit into the concave inner surfaces of the fifth myomere.

Having obtained a sequence of views of a series of consecutive myomeres, let us proceed to reconstruct from them the conformation of a single myomere. As the ventral moiety of a myomere is the counterpart of the dorsal, it will be sufficient to confine our remarks to the latter.

It is evident from the foregoing observations that a myomere is not visible superficially in its most anterior region. We have seen it (6) as a triangular area in the angle between the centrum and the horizontal septum. By dissection it is easy to demonstrate that this triangle represents the base of a pyramid which converges to an apex on the centrum *. Tracing the sixth myomere backwards through the width of a myomere, we should find it to show the appearance of No. 5 in the text-figure ; it has then been thrust from contact with the vertebral column by the appearance of a new pyramid : moreover, it has made its anterior superficial appearance dorsally. Backwards again through the width of another myomere it has the appearance of No. 4 ; here a considerable portion of it is visible externally, both dorsally and just above the "red fibres"; in this and in its next stage, No. 3, it appears in section as two quadrangular faces which are approaching one another. In No. 2 we are able to see how the two faces, whose superficial continuations are now recognisable as the mesio-dorsal (*M.D.*) and latero-dorsal (*L.D.*) portions respectively, become confluent. Passing from this point through the width of another myomere the two faces are found fused into one triangular area (1, in section), which is invisible externally owing to the convergence of the faces of the myomere next in front. By dissection it can be demonstrated that this triangle forms the base of a pyramid whose apex is attached to the vertical septum.

Thus it is seen that the dorsal moiety of a myomere is composed of two opposed hollow pyramids, a dorsal one directed inwards and backwards, and a ventral one directed inwards and forwards. They are not divided by a septum but share a common face, which may be seen in the text-figure at the areas marked 2, 3, 4, and, in part, 5 in the *L.D.* portion of the section †.

The ventral moiety of the myomere takes a course symmetrical with the dorsal, which it resembles in all essential points of structure.

Before leaving this figure it would be well to observe that it serves admirably to indicate why there is but one change in direction of the external fibres, correlated with the change which the conical structure involves, in each moiety of the myomere, instead of the two which one would be led to expect. Following the central course of myomere No. 4, it is seen that only the fibres above the mesial plane of the *L.D.* portion, and below that of the *L.V.* portion, are visible at the surface. The fibres below the mesial plane of the *L.D.* portion and above that of the *L.V.* portion, which take the opposite directions respectively to those named in the preceding sentence, are only found in myomeres 5 and 6 ; and these do not appear on the surface.

I have also followed the course of the myomeres in the dorsal moiety of a young Salmon through over a hundred consecutive sections from the pelvic region. Two such sections are reproduced here (text-fig. 3) to indicate the directions of growth and diminution in seven consecutive myomeres. As corroborative

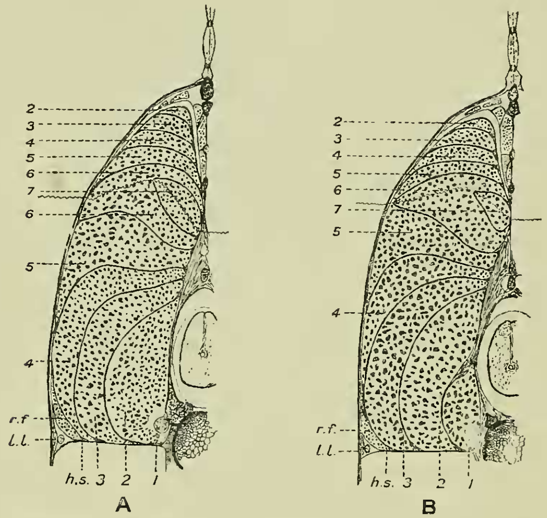
* This will be corroborated in the remarks on sections of a young Salmon, p. 334.

† It is evident that this area may be regarded as the forward continuation of a pyramid similar to 1, or as the backward continuation of a pyramid similar to 6.

evidence of the above observations the figures speak for themselves; but the essential features which I wish to emphasize are these:—

First, that the horizontal septum (*h.s.*) running from the lateral line to the vertebral centra is continuous; also that the "red fibres" (*r.f.*) remain constant in position and extent, thereby showing that they form no part of the system of pyramids or cones.

Text-figure 3.




Two transverse sections through the dorsal moiety of the lateral muscle of a young Salmon (34·5 mm.) taken from the pelvic region.

A represents a plane ·064 mm. anterior to B; 1–7, series of myomeres, identical in both sections; *h.s.*, horizontal septum; *l.l.*, lateral line; *r.f.*, "red fibres" ~~~~, arbitrary internal division-plane between the mesio-dorsal and latero-dorsal portions.

Secondly, that the numbers are not merely written down symmetrically on either side of an arbitrary starting point. Where any two parts of myomeres are numbered as the same myomere, this has actually been proved to be the case by tracing their passage through a sufficient number of sections until they become confluent one with the other; to take an example, the separate parts denoted by the number 5 in A, become confluent when traced backwards to their position in B 5.

Thirdly, that the ventral, forwardly directed pyramid is seen at its origin at A 1, and again, considerably increased in bulk, when traced backwards to its position at B 1; conversely, that the dorsal posteriorly-directed pyramid is seen decreasing from A 7 to B 7.

Fourthly, that at the outermost extremity of myomere B 6 (at the point where it is cut by the index line of B 7) we find, very nearly*, the apex of one of the external backwardly-directed V-shaped myocommata. It has been pointed out that an imaginary line joining such apices forms the division between the mesio-dorsal and latero-dorsal portions of the surface area. It is now apparent that any deep continuation of this superficial division must also be guided by expediency; for, internally to our superficial guide-point, we find a <-shaped area (the section of a hollow pyramid), which may be regarded in its entirety as part of a dorsal, posteriorly-directed pyramid, and so of the mesio-dorsal portion of the muscle; or, with equal justice, its lower arm may be regarded as part of the latero-dorsal portion, from the fact that its fibres follow the same direction as those in that portion.

The question to be decided is this: granted that such a division of the lateral muscle is in either case an arbitrary one, is it expedient to frame it in terms of pyramidal masses or in terms of direction of fibres?

Before answering this question let us examine the fissure which divides the mesio-dorsal and the latero-dorsal portions near their anterior origins on the skull. It is found here that all the fibres above the cleft throughout its depth run in the same direction, namely, from above anteriorly to below posteriorly, and that all those below it take the opposite direction. That is to say, when they split apart, the two portions are not divided according to their pyramidal structure, but according to the direction of their fibres; and this fact indicates that the division of the dorsal moiety of the lateral muscle into a mesio-dorsal longitudinal mass and a latero-dorsal longitudinal mass can most naturally be framed in terms of the direction of its component fibres.

In text-fig. 3, B it has been pointed out that the index-line to the 7th myomere cuts the skin approximately at a point in the superficial line of division of the mesio-dorsal and latero-dorsal portions. From this point inwards a zigzag line has been drawn to indicate the arbitrary internal division-plane between the mesio-dorsal and latero-dorsal portions; above this plane the fibres are inclined upwards and forwards, below it they are inclined downwards and forwards. In A the superficial division can be found by bisecting the line of skin between the two portions of the myocomma which encloses the 6th myomere; from this point the internal division-plane can be traced as in B.

It will now be realised that by somewhat devious paths we have reached Gegenbaur's position with regard to the structure of the dorsal moiety of the lateral muscle (*cf.* p. 320). Our arbitrary division leaves us with a series of incomplete cones, or

* In the section next in front of this the apex of the sixth myomere is actually in the surface.

rather pyramids, whose apices are directed backwards, and, below them, a series of complete pyramids whose apices are directed forwards.

The incomplete pyramids correspond externally with Humphry's mesio-dorsal portion, and the complete pyramids with his latero-dorsal portion. For descriptive purposes this division of the dorsal moiety (which is equally applicable to the ventral moiety) has its uses. At the same time one cannot insist too strongly on the fact that its morphological basis is only slightly more secure than that on which Humphry and Maurer framed their two-layer hypothesis; both views depend upon the direction of muscle-fibres, but the former derives certain additional support from an investigation of the muscles in their most anterior region.

The apices of the ventrally-directed pyramids do not always rest against the vertebral centra, but in some Teleosteans (*Scomber*, *Trigla*) they originate in the midst of the muscle-mass. In this case the pyramids become converted into true cones, and in section they appear as a series of concentric circles. In rarer instances (*Conger*) the apices of the dorsal backwardly-directed pyramids are also similarly situated, and in a section of the dorsal moiety of the lateral muscle two superimposed series of concentric circles appear.

## Summary.

1. The body-wall of a Teleostean fish is composed on either side of a series of transverse muscles (myomeres) divided from one another by fasciæ of connective-tissue (myocommata).

For practical purposes these may be regarded collectively as forming a single lateral muscle.

2. The lateral muscle is composed of a single layer, which varies considerably in thickness in different parts of the body.

3. In its primary condition, such as obtains in the caudal region, it is divided into two symmetrical longitudinal moieties, which are separated by a horizontal septum passing from beneath the lateral line to the vertebral column.

4. The dorsal moiety is marked externally by a series of backwardly directed >-shaped bands. By joining the apices of these >'s an imaginary line is formed dividing the dorsal moiety into a (dorsal) mesio-dorsal portion and a (ventral) latero-dorsal portion. In the mesio-dorsal portion the muscle-fibres run from above anteriorly to below posteriorly; in the latero-dorsal portion they take the opposite inclination.

Internally the mesio-dorsal portion is recognised as a series of incomplete hollow pyramids, or cones, whose apices are directed posteriorly; while the latero-dorsal portion is composed of a series of complete hollow pyramids, or cones, whose apices are directed forwards.

The ventral moiety is likewise divided into a (dorsal) latero-ventral portion and a (ventral) mesio-ventral portion. The fibres of the latter, at first oblique, as they approach the middle line become straight, and resemble a rectus.

5. The above divisions of the dorsal and ventral moieties suffice for descriptive purposes; but, pending further evidence, they must be regarded as essentially empirical in nature.

6. Small cylindrical longitudinal muscles are frequently cut off from the mesio-dorsal portion, along the mid-dorsal line in the interspaces of the dorsal fins. These are the supracarinales of Owen.

Similar muscles are frequently cut off from the mesio-ventral portion along the mid-ventral line. These are the infracarinales of Owen.

7. A small muscle, whose fibres are usually distinguished by their red colour, is cut off from the latero-dorsal portion and occupies the slope of the furrow in which the lateral nerve is situated.

A corresponding muscle is cut off from the latero-ventral portion immediately below the lateral line.

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